Intratrial Cue Observations and Delayed Response Performance in Normal and Prefrontal Monkeys

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When they were restrained during testing prefrontal squirrel monkeys were found to be deficient with respect to normal controls in their performance on two variations of an indirect delayed response test. Three measures of the intratrial cue observations of prefrontal and normal monkeys were studied. The latency for the first rewarded cube observation was the same for prefrontal and normal monkeys throughout DR testing. Stimulus observation during the cueing period of DR testing was also similar for normal controls and prefrontal operates. Furthermore, stimulus observation during the delay period of DR testing did not vary as a function of lesion. Prefrontal and normal monkeys were comparable in their intratrial cue observations on DR even when their overall performance levels differed greatly. It was concluded that intratrial cue-observation was not related to DR test performance.

INTRODUCTION

Buddington et al. (1969) studied the performance of normal and prefrontal squirrel monkeys on discrimination and indirect delayed response (DR) tests. It was found that the introduction of an intratrial delay, into a testing procedure that was otherwise unchanged from previous discrimination tasks, resulted in decreased levels of both prefrontal and normal performance. Furthermore, the efficiency with which criterion performance was reattained during initial DR testing was dependent upon the cueing situation for prefrontal operates, but not for normal controls. A further analysis of their data revealed that neither the cueing situation presented during DR testing nor the effect of introducing the delay could, in themselves, sufficiently account for the DR performance of prefrontal operates. Rather, it was the interaction of the cue situation with the effect of introducing the intratrial delay which determined whether prefrontal DR performance would be comparable or inferior to that of normal controls.

Considering the decreased level of performance for all animals during initial DR testing Buddington et al. (1969) hypothesized that, with the introduction of an intratrial delay, modification of the response patterns previously established during discrimination training was necessary.

This hypothesis was investigated in the present report by comparing the average behavioral pattern during individual discrimination and DR test-trials with the overall level of performance. By obtaining these two measures during selected portions of the testing sequence, variations of performance-level across tasks could be related to concomitant alterations of within-trial behavior. With this approach, and by employing the testing sequence described by Buddington et al. (1969), it would be possible to identify the hypothesized modification of within-trial behavior during initial DR testing, as well as to compare prefrontal and normal within- and between-trial behaviors, when adaptation to the introduction of an intratrial delay was occurring.

For the purposes of thepresent investigation, within-trial behavior was limited to a single response variable. The animals were restrained during testing with the permitted intratrial behaviors being related primarily to cue observation (head movement) or reward attainment (hand, arm, and some torso movement). Because previous investigations (Miles and Blomquist, 1960; Buddington et al., 1969) have reported that prefrontal damage does not alter the motor behavior of squirrel monkeys, it was expected that the motor acts involved in reward attainment would be similar for the prefrontal and normal squirrel monkeys in the present study. The pattern of within-trial behavior was therefore expressed in terms of a single intratrial behavior (i.e., amount of cue observation).

The second objective of this study was a further investigation of the relationship between cue situation and delay introduction. As was mentioned above, the interaction of these two factors was found to determine whether prefrontal performance during DR testing was comparable, or inferior, to that of normals (Buddington, et al., 1969). On the basis of this result these same authors hypothesized that dorsolateral prefrontal damage in the squirrel monkey resulted in an increased dependence upon external cues for the guidance of behavior when modification of response patterns (the hypothesized effect of delay introduction) was required. This hypothesis was studied in the present investigation by comparing prefrontal and normal intratrial cue observations during the initial DR tests for the training sequence.

METHOD

Subjects

Twelve naive adult male squirrel monkeys (*Saimiri sciureus*) served as subjects. All animals were housed throughout the experiment in individual cages permitting some degree of communication with neighbors. Six monkeys were randomly assigned to the normal control group and six animals received damage to the dorsolateral prefrontal cortex.

Surgery

All operations were performed under aseptic conditions as described elsewhere (Buddington et al., 1969). The intention was to ablate the region of the *sulcus principalis* of the prefrontal cortex. Animals in the operated group were allowed either a one-month or a two-year recovery period between operation and the commencement of any experimental procedures.

Apparatus

A modification of the Wisconsin General Test Apparatus (Harlow, 1959) was utilized. The compartment containing the monkey was 43 cm. deep, 56 cm. wide and 87 cm. high. A Plexiglas monkey perch extended from one side of the animal compartment to the other and could be adjusted in the vertical plane from 8 to 20 cm. below the surface of the stimulus tray. An

eyehook was located on the animal compartment floor 30 cm. behind, and 30 cm. below, the monkey perch.

The stimulus tray which remained stationary in a position forward and towards the monkey compartment contained two foodwells 1.6 cm. in diameter and spaced 31.8 cm. apart. Each foodwell was covered by a 3.8 cm. cube constructed with translucent Plexiglas. The cubes were each attached to the stimulus tray by two lightweight chains, one chain fastened to the back lower edge of the cube and the other fastened to the lower edge of the cube-side facing away from the monkey. Inside each cube was a miniature 6 volt light bulb (Westinghouse number 47 - radio) which was controlled by a switchbox outside of the apparatus. The bulbs were held by sockets mounted in the rear wall of each cube with all external wiring concealed from the animal's view.

An opaque screen and a transparent Plexiglas screen, both of which could be raised or lowered, separated the monkey from the stimulus cubes. These screens were constructed so that when they were lowered a center area of the stimulus tray 25 cm. wide, 22 cm. high, and 18 cm. deep was left open to the animal compartment. A snaphook was fastened to a metal post in the center of this area. Located 20 cm. from this post, within the stimulus tray compartment, was an Arriflex 16-S 16 mm. motion picture camera. The camera was equipped with a 10 mm. wide-angle lens which protruded through a closely fitted opening in an opaque barrier directly in front of the camera. A black curtain on either side of the camera

barrier allowed the experimenter to bait the foodwells during the intratrial interval without being observed when he subsequently raised the opaque screen separating the monkey from the stimulus tray compartment. Located 10 cm. in front of the camera was a timer-light which flashed once each second. The camera which was set at a speed of eight to ten frames per second was controlled by a microswitch that was activated when the opaque screen separating the animal from the stimulus tray compartment was raised. The apparatus was illuminated by a 25 watt flourscent ceiling light in the stimulus tray compartment, and by a 25 watt incandescent bulb in a photoflood reflector at the rear of the animal compartment. The test-trials were recorded on 100-foot rolls of Kodak Tri-X, black and white reversal film.

Each animal wore loosely fitting, lightweight, neck and waist chains (American Chain and Cable Company number 16, single brass jack chain) 95 cm. and 56 cm. respectively, in length. A snaphook was fastened tightly to the end of each chain. An 85 cm. section of wooden pole with an eyehook on either end allowed for handling of the animals between home cage and test apparatus.

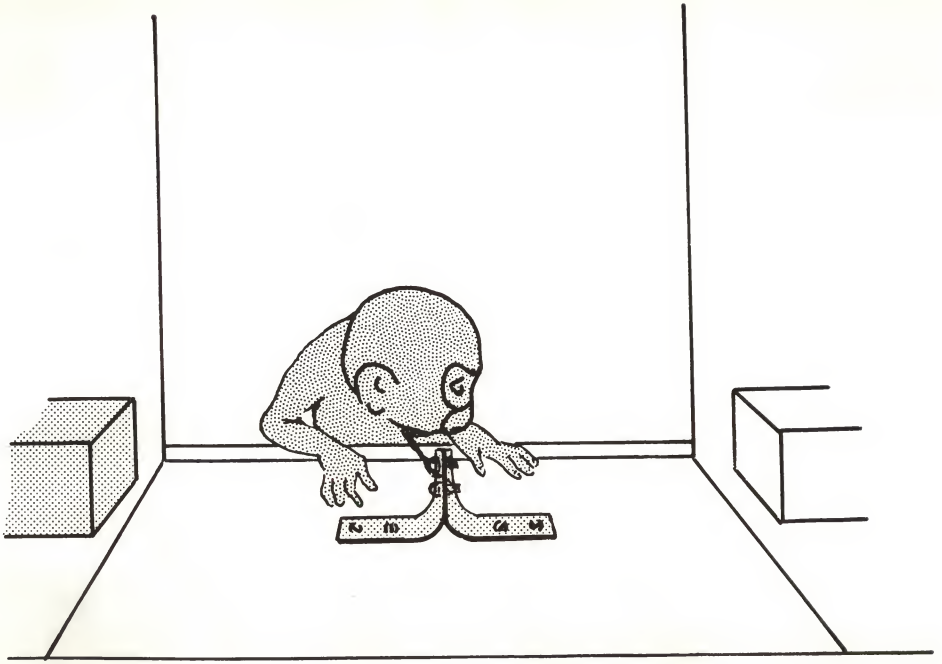
Procedure

Habituation.--Each monkey was gradually habituated to being handled and restricted by his neck and waist chains. During the first habituation day the monkey was transfered from his home cage to the apparatus cubicle by attaching his neck chain to the handling pole. The monkey was then offered

as many currants as he would eat before being returned to his home cage. During the second and third habituation days the monkey was placed in the apparatus and began eating currants while sitting on the Plexiglas perch. The waist chain was attached to the eyehook on the animal compartment floor during this period but the neck chain remained on the handling pole. After attaching the waist chain, during the final habituation day, the monkey's neck chain was threaded through the snaphook in the center of the stimulus tray, then removed from the handling pole and brought down under the perch to be snapped onto the eyehook in the animal compartment floor. Restrained in this manner (see Figure 1), the monkey was given currants on the stimulus tray until satiated. No subsequent procedure was begun for any animal until he had completed this habituation sequence.

Shaping.--Prior to testing, each animal was given a minimum of five days' training in displacing one or another of the unlit stimulus cubes for a currant placed in the foodwell beneath the cube. On successive trials, one of the cubes was placed over the baited foodwell while the other was positioned at the rear of the tray behind the unbaited foodwell. Currant placement was determined by a restricted Gellerman (1933) series. There were 40 trials a day until the last two days of shaping when there were 60 trials. In no case was testing begun until the subject responded without hesitation to cube presentation for 120 trials during two consecutive days. The last 60 shaping trials of every

Figure 1. A schematized representation of the fully restrained animal as he would have appeared in the camera viewfinder when he was observing the rewarded cube. The monkey is separated from the stimuli by two translucent Plexiglas doors, and is attached to the center post by a neck chain.



animal were filmed. Each animal was restrained in the apparatus just prior to the daily test-session in this and all subsequent procedures.

Discrimination training.--When an animal reached the shaping criterion, discrimination training (DT) was begun. A currant was placed in one foodwell and both stimulus cubes were positioned covering their respective wells. Location of the baited well was determined by the same Gellerman series used in shaping. Each DT trial commenced by raising the opaque screen separating the animal and the stimulus cubes. A two-second observation period was subsequently allowed during which the transparent Plexiglas screen remained in place allowing the animal to view, but not manipulate, the cubes. At the end of the observation period the baited cube was immediately illuminated to begin a two-second cue period. During the cue period, the Plexiglas screen remained in place preventing manipulation of the stimulus cubes. At the end of the cue period the transparent screen was immediately removed and, with one cube lit and the other darkened, the animal was allowed to respond. A trial was begun every 45 seconds and the non-correction technique was employed. The lit cube was positive for all animals (i.e. a currant was placed in the foodwell beneath it). Each animal was tested daily for as many trials as could be recorded on a single 100-foot roll of film. On a single day during DT there were never fewer than 45, nor more than 60, test-trials for any animal. All animals were

trained to the criterion of 36 correct responses in any block of 40 trials. On the day criterion performance was achieved the next test in the sequence was immediately begun.

Stimulus manipulation.--Prior to the beginning of the experiment the normal and operated animals were randomly assigned to either an A or a B subgroup (three normal controls and three prefrontal operates per subgroup). When an animal in Group A reached criterion on DT it was tested on two successive stimulus manipulations (STM). The procedure during STM training was identical to DT for the observation and cue periods. Therefore, when the transparent screen was about to be raised at the beginning of the response period during STM, one cube was lighted and the other was unlit. However, as the screen was raised during STM (zero delay) the unlighted cube was illuminated and the monkey was presented with two lit cubes. When criterion had been reached on this first STM, training on the second began. Testing conditions were identical to those present during the first STM, except that the illuminated cube went out as the transparent screen was removed. The animals in Group A were therefore faced with two darkened cubes at the time of response execution during the second STM.

Group B, after reaching criterion on DT, was presented with the same two STMs as Group A, but in reverse order.

Throughout all STM procedures, the cube which was illuminated during the two-second cue period was rewarded. The performance criterion and number of daily test-trials

were the same as described for DT.

Delayed response.--Delayed response (DR) testing was begun for each animal as soon as it had reached criterion on the second STM. The procedure for DR testing was the same as that for the STM tasks except that the transparent screen remained in place for an additional two seconds when the stimulus manipulation occurred at the end of the cue period. On the first DR test both cubes were darkened during this two-second delay period and at the time of response execution for Group A animals. For their second DR task Group A animals were presented with two illuminated cubes during the delay period. Group B animals received the same two DR tasks, but in reverse order. As in all previous tests, criterion performance was 36 correct responses in any block of 40 trials, and the cube illuminated during the cue period was positive. Training on the second DR task began for each monkey as soon as it had achieved criterion performance on the first DR test. If an animal had not attained criterion within 500 trials on the first DR test, training on the second DR task began immediately.

Food deprivation.--For approximately one hour following daily testing, all animals were provided with a diet of standard, small monkey, lab chow supplemented twice weekly with portions of apples and oranges. Subjects were consequently 22-23 hours food deprived at the beginning of each daily training session. In addition to this deprivation schedule the amount of food provided at the daily feeding

hour was adjusted for each animal so that, by the time he started discrimination training, he readily accepted 60 currants during each daily test-session.

Histology.--At the end of the experiment each operated monkey was sacrificed and perfused with saline followed by 10 percent formalin. The brains were subsequently removed and photographed from the dorsal view to verify the locus of damage within the prefrontal areas.

Data analysis.--Since DT testing conditions were the same for all animals, these data were withheld from the overall trials-to-criterion analysis and the combined A and B normal subgroups compared with the A and B prefrontals in a separate DT analysis. The remaining data were analyzed by means of a four-way repeated-measures analysis of variance. The factors were designated as (a) task, i.e., STM versus DR; (b) stimuli, i.e., cubes on versus cubes off; (c) order, i.e., both cubes on for the first test of a task followed by both cubes off versus cubes off and then cubes on; and (d) lesion, i.e., normals versus prefrontals.

Discriminanda observations were analyzed for the cue period during DT and STM and for both the cue and delay periods during DR. The observation data for the cue period during STM and DR were analyzed by means of a six-way repeated-measures model. Four of the factors (task, stimuli, order, and lesion) were the same as described for the trials-to-criterion analysis. The remaining factors were designated

as (a) trials, i.e., the first versus the last twenty trials of each STM or DR test; and (b) cue contingency; i.e., the rewarded versus non-rewarded cube.

The observation data for the cue period during DT were analyzed with a three-way repeated-measures model. Because the DT testing conditions were the same for all animals the combined A and B normal subgroups could be compared with the combined A and B prefrontals. The factors were therefore designated as (a) lesion; (b) trials; and (c) cue contingency, with the same definitions as their counterparts in the above-described analyses.

Cue observation during the delay period on DR testing was analyzed as a five-way repeated-measures design. The factors, which were designated as (a) order; (b) lesion; (c) stimuli; (d) trials; and (e) cue contingency, were defined as in the previously described data analyses.

The latency of the first rewarded cube observation during the cue period was analyzed with a three-way repeated-measures model. The factors were designated as (a) order, i.e., Group A prefrontal and normal monkeys versus Group B; (b) lesion, i.e., prefrontal operates versus normal controls; and (c) latency; i.e., for the entire test sequence the total average latency of the first rewarded cube observation based upon selected 20 trial blocks from each task.

A second analysis of the DR latency data was conducted employing a four-way repeated-measures design. The factors were designated as (a) order, i.e., Group A prefrontal

and normal monkeys versus Group B; (b) lesion, i.e., prefrontal operates versus normal controls; (c) stimuli, i.e., both cubes illuminated during the delay versus both cubes darkened; (d) trials, i.e., the first versus the last twenty trials of each DR test.

RESULTS

Behavior

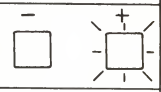
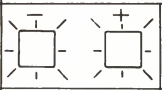
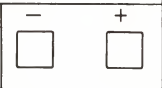
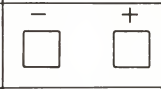
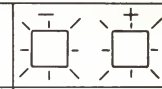
Recovery period.--The prefrontal operates provided with the twelve-month recovery period (SM 374, 376, and 379) and those with the one-month recovery period were randomly assigned to Subgroups A and B. Although the twelve-month group was inferior to the one-month group on DT, the overall performance of the two groups was not consistently different and did not affect the statistics or interpretation of the study.

Trials to criterion.--The number of trials each monkey required to reach criterion is presented for each of the testing conditions in Figure 2.

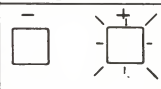
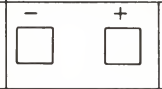
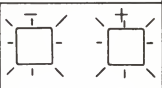
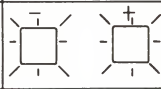
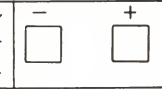
The combined A and B prefrontal subgroups were not significantly different from the combined normal subgroups on DT ($t=1.30$, $p > 0.20$). For the analysis of variance conducted on the STM and DR trials-to-criterion data there were four main effects, six two-way interactions, four three-way interactions, and one four-way interaction. The lesion (L) and task (T) main effects were both significant at the 0.01 level of confidence ($F=17.27$ and 51.66, $df=1/8$ for each test). The L X T interaction was significant at the 0.02 confidence level ($F=9.35$, $df=1/8$). All other main effects and interactions for this analysis were not significant.

Figure 2. Trials to the 90 percent criterion. (The stimulus cues present when the manipulanda were presented to the animal are indicated schematically at the top of each column for Groups A and B. Lines drawn around a cube indicate that it was illuminated, while a + above a cube indicates that the reward was located in the foodwell beneath it. The task abbreviations at the top of each column are the same as in the text. Following a trials-to-criterion score, + indicates that testing was discontinued after the number of trials indicated. All scores include the criterion trials).

GROUP A

TASK	DT	STM		DR	
STIMULUS SITUATION					
NORM. SM 366 SM 402 SM 413	113 194 $\bar{X}$ = 188 254	40 38 $\bar{X}$ = 42 47	40 41 $\bar{X}$ = 40 38	40 148 $\bar{X}$ = 76 40	167 90 $\bar{X}$ = 101 45
FRONT. SM 379 SM 412 SM 414	344 143 $\bar{X}$ = 220 173	41 40 $\bar{X}$ = 58 93	52 36 $\bar{X}$ = 42 39	481 500+ $\bar{X}$ = 397 211	500+ 500+ $\bar{X}$ = 400 201

GROUP B

TASK	DT	STM		DR	
STIMULUS SITUATION					
NORM. SM 384 SM 399 SM 445	190 159 $\bar{X}$ = 161 134	111 38 $\bar{X}$ = 62 36	37 40 $\bar{X}$ = 38 37	263 412 $\bar{X}$ = 286 184	38 43 $\bar{X}$ = 99 217
FRONT. SM 374 SM 410 SM 376	208 189 $\bar{X}$ = 224 274	55 40 $\bar{X}$ = 111 239	63 47 $\bar{X}$ = 60 71	263 307 $\bar{X}$ = 237 142	500+ 38 $\bar{X}$ = 346 500+

Cue observation.--The data for discriminanda observation during the cue period of each task are presented in Table 1. For DT, the analysis of observations during the cue period had three main effects, three two-way interactions and one three-way interaction. The cue contingency (C) main effect ($F=59.62$, $df=1/10$) and the C X trials (TR) interaction ($F=35.35$, $df=1/10$) were both significant beyond the 0.01 level. All other main effects and interactions for this DT analysis were not significant. The statistical analysis of observations during the cue period for STM and DR testing had six main effects, fifteen two-way interactions, twenty three-way interactions, fifteen four-way interactions, six five-way interactions, and one six-way interaction. The task (T), stimuli (S), and cue contingency (C) main effects were all significant beyond the 0.01 level while the trials (TR) main effect was significant at the 0.025 confidence level ($F_T=39.55$, $F_S=12.06$, $F_C=230.09$, $F_{TR}=7.57$, $df=1/8$ for each test). The significant two-way interactions were T X TR ($F=11.84$, $df=1/8$, $p=0.01$) and T X C ($F=9.23$, $df=1/8$, $0.01 < p < 0.025$). Of the significant three-way interactions, lesion (L) X S X TR and T X TR X C were both significant at the 0.05 confidence level ($F=5.39$ and 5.69, respectively, and $df=1/8$ for each test), while order (O) X S X C was significant at the 0.025 level ($F=10.79$, $df=1/8$). All other main effects and interactions for this analysis were not significant.

The data for cue observations during the delay period of DR testing are presented in Table 2. The statistical

Table 1. Cue Period: Average Number of Motion Picture Frames Showing Cube Observation[@]

GROUP A

Task	Discrimination				Stimulus Manipulation			
Stimulus Cubes	One Cube Illuminated				Both Cubes Illuminated			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed	R*	N**	R	N	R	N	R	N
Normals	7.3	6.3	10.8	4.0	10.1	5.1	9.5	4.0
Frontals	5.1	5.6	9.6	4.0	8.5	3.8	10.6	2.6

GROUP B

Task	Discrimination				Stimulus Manipulation			
Stimulus Cubes	One Cube Illuminated				Both Cubes Unlit			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed	R	N	R	N	R	N	R	N
Normals	5.2	4.6	8.3	4.4	8.6	3.3	8.3	3.0
Frontals	6.5	7.8	8.8	3.4	8.5	4.7	9.8	3.2

*R=Rewarded stimulus cube

**N=Unrewarded stimulus cube

[@]The raw scores for these data are presented in the Appendix

Table 1. continued

Stimulus Manipulation				Delayed Response				Delayed Response			
Both Cubes Unlit				Both Cubes Unlit				Both Cubes Illuminated			
First 20		Last 20		First 20		Last 20		First 20		Last 20	
R	N	R	N	R	N	R	N	R	N	R	N
8.8	4.5	9.8	4.1	9.9	3.2	8.4	4.6	7.2	4.1	6.7	2.9
10.9	3.1	10.7	3.1	9.3	3.7	8.9	2.5	8.4	3.0	6.8	3.7

Stimulus Manipulation				Delayed Response				Delayed Response			
Both Cubes Illuminated				Both Cubes Illuminated				Both Cubes Unlit			
First 20		Last 20		First 20		Last 20		First 20		Last 20	
R	N	R	N	R	N	R	N	R	N	R	N
7.7	2.5	8.5	2.3	8.2	3.3	7.0	2.5	6.8	3.0	7.4	2.7
9.1	3.2	9.6	3.0	8.2	3.1	7.3	2.8	8.7	5.0	5.4	3.8

Table 2. Delay Period: Average Number of Motion Picture Frames Showing Cue Observation @

GROUP A

Task	Delayed Response				Delayed Response			
Stimulus Cubes	Both Cubes Unlit				Both Cubes Illuminated			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed	R*	N**	R	N	R	N	R	N
Normals	8.7	2.6	7.3	2.5	6.5	3.7	6.4	2.0
Frontals	6.6	4.0	7.0	2.1	6.9	3.5	5.4	3.5

GROUP B

Task	Delayed Response				Delayed Response			
Stimulus Cubes	Both cubes Illuminated				Both Cubes Unlit			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed	R	N	R	N	R	N	R	N
Normals	6.8	4.6	6.0	3.1	5.9	2.4	6.4	1.9
Frontals	7.7	3.3	7.2	2.6	7.5	3.4	5.7	2.4

*R=Rewarded Stimulus Cube

**N=Unrewarded Stimulus Cube

@The raw scores for these data are presented in the Appendix

analysis for these data had five main effects (order, lesion, stimuli, trials, and cue contingency) and a total of 26 interactions. The cue contingency and the trials main effect were each significant beyond the 0.01 confidence level ($F=18.66$ and 57.62 respectively, $df=1/8$ for each test). The five-way interaction of the factors designated as main effects was also significant ($F=9.04$, $df=1/8$, $0.01 < p < 0.025$). All other main effects and interactions for these analyses were not significant.

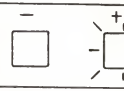
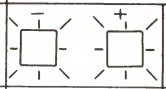
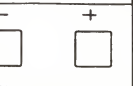
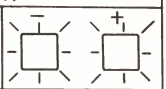
The average latency of the initial rewarded cube observation during the first and/or last twenty trials of each task is presented in Figure 3. None of the main effects or interactions were statistically significant for either of the variance analyses conducted on these data.

Histology

A dorsal view of the brain from each prefrontal operate is presented in Figure 4. From the gross brain specimens, bilateral damage to the prefrontal areas of SMs 374, 376, 379, and 412 appeared to be similar in extent and located within the area of the sulcus principalis as intended. Damage to the prefrontal area in the right hemisphere of SMs 410 and 414 was as intended and was similar in extent and locus to the damage sustained by the other operates. Damage to left prefrontal areas however was less extensive than intended for these latter two animals. In the case of SM 410 damage appeared to be located in a medial and anterior position within the dorsal prefrontal cortex of the left

Figure 3. Average Latency of the Initial Rewarded Cube Observation. (The column and row headings are the same as for Figure 2 except that the individual animals are not listed. The number given for the first and/or last twenty trials of each test is the group average for the number of motion picture frames, counting from the beginning of the cue period, until the initial positive cube orientation. The scores in parentheses present the range for each mean).

GROUP A

TASK	DT		STM		DR			
STIMULUS SITUATION								
NORMALS	FIRST 20 7.3 (6.7-8.3)	LAST 20 6.9 (6.6-7.4)	LAST 20 7.0 (6.3-8.3)	LAST 20 7.3 (6.9-8.0)	FIRST 20 5.5 (3.9-8.6)	LAST 20 6.2 (5.6-7.8)	FIRST 20 5.6 (4.0-7.4)	LAST 20 7.1 (4.7-10.3)
FRONTALS	FIRST 20 10.3 (7.2-13.6)	LAST 20 7.4 (4.5-9.8)	LAST 20 5.9 (5.3-7.0)	LAST 20 5.4 (4.2-6.9)	FIRST 20 7.6 (4.4-12.0)	LAST 20 6.9 (5.6-8.4)	FIRST 20 8.3 (6.7-11.0)	LAST 20 11.6 (7.2-15.0)

GROUP B

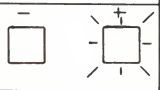
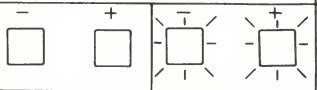
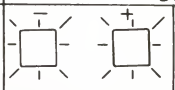
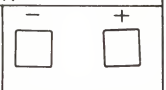
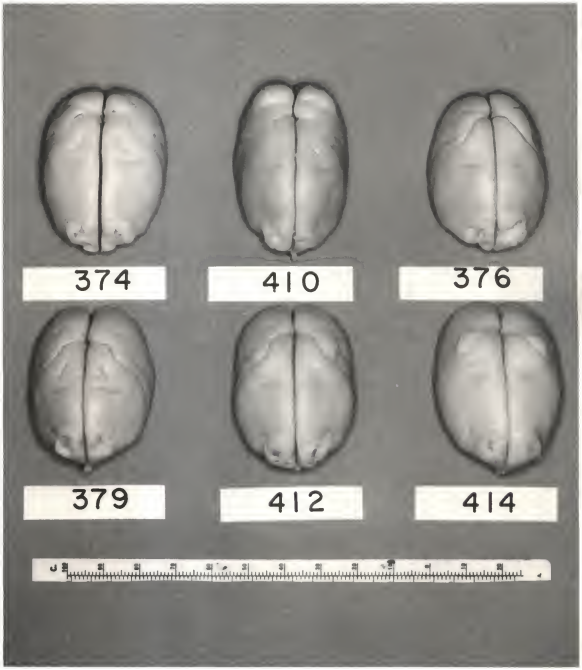
TASK	DT		STM		DR			
STIMULUS SITUATION								
NORMALS	FIRST 20 8.4 (6.2-10.6)	LAST 20 6.5 (5.5-7.2)	LAST 20 4.9 (4.1-5.9)	LAST 20 5.3 (3.5-7.2)	FIRST 20 6.2 (3.7-8.9)	LAST 20 6.5 (4.5-8.0)	FIRST 20 7.7 (6.2-9.9)	LAST 20 8.5 (6.8-10.7)
FRONTALS	FIRST 20 8.4 (6.5-10.3)	LAST 20 8.6 (4.2-12.6)	LAST 20 7.7 (5.8-11.6)	LAST 20 6.4 (3.7-9.1)	FIRST 20 8.0 (3.9-13.3)	LAST 20 8.0 (6.2-10.5)	FIRST 20 9.2 (6.4-11.7)	LAST 20 7.8 (6.6-8.7)

Figure 4. A dorsal view of the brain from each prefrontal operate.


374
410
376
379
412
414

hemisphere leaving the major portion of the sulcus principalis intact. Injury to the left prefrontal cortex of SM 414 was more correctly located, but removal of the sulcus principalis was less than total. As can be seen by reference to the trials-to-criterion data (Figure 2), these variations in lesion locus and size were correlated with test performance. In particular, the DR performance for SM 410, with an essentially unilateral sulcus principalis removal, was comparable to the DR performance of the normal controls in Group B. The DR performance of the remaining Group B operates, however, was deficient in comparison to normal controls. The DR performance of SM 414 was impaired in comparison to Group A normal-control performance. This animal was, however, less impaired on DR than the remaining Group A prefrontals with more complete bilateral sulcus principalis removals. These lesion variations had the effect of increasing between-subjects variability on the DR tests (e.g., see Figure 2, Group B prefrontal operates on their second DR test), but did not otherwise alter the results or interpretation of the study.

DISCUSSION

Trials to Criterion

As indicated by the significant lesion main effect, prefrontals were poorer in their overall STM and DR performance than normals. This same tendency was also present on DT, although prefrontals were not statistically different from normals. These results are in agreement with a previous investigation (Buddington et al., 1969) where unrestrained monkeys were observed in an identical testing situation.

The task main effect indicates that the DR tests were significantly more difficult than STM for both normal and prefrontal monkeys. As shown by the significant L X T interaction, however, this increase in difficulty between STM and DR was greater for prefrontal operates than normal controls.

It is concluded on the basis of these results that there is a general, debilitating effect of the lesion resulting in the overall inferiority of prefrontal operates on discrimination and discrimination-based tasks. It is further concluded that there is a second, task-specific effect of the lesion resulting in especially deficient prefrontal DR performance. Whether these effects are related or separate could not be decided on the basis of the present investigation.

The DR performance for prefrontal monkeys restrained during testing is not the same as the performance of monkeys free to roam an animal compartment. Buddington et al. (1969) reported that unrestricted prefrontal operates were impaired in comparison to normal controls when their first DR test was with the cubes off stimulus situation. When subsequently tested with both cubes illuminated during the delay prefrontal monkeys were observed to perform as well as normal controls. In the present study, prefrontal operates tested with this same stimulus sequence (see Figure 2, Group A prefrontals) were impaired throughout DR training. Furthermore, Buddington et al. (1969) reported that non-restrained prefrontal operates were unimpaired when tested on DR with the both cubes on followed by the cubes off stimulus situations. When prefrontal operates were tested with this same cue sequence in the present investigation they were comparable to normal controls on their first DR test (cubes "on") but were deficient when subsequently tested with two darkened cubes (see Figure 2, Group B prefrontals). It is concluded on the basis of these comparisons that eliminating locomotor behavior during testing increases the severity of prefrontal impairment on DR tasks.

The DR performance of restrained normal monkeys, tested with both cubes darkened during the delay, did not appear to be different from the performance reported by Buddington et al. (1969) for unrestricted normal animals during cubes off DR testing. Restraining the monkeys did, however, appear

to increase the number of trials normal animals took to reach criterion on DR training when both cubes were illuminated during the delay. This increase in the number of trials to criterion was not as large for the normal subjects as it was for the prefrontal monkeys that were tested on DR with two illuminated cubes. The debilitating effects of eliminating locomotor behavior during DR testing were therefore much less severe and pervasive for normal controls than prefrontal operates. It is therefore concluded that the DR performance of prefrontal squirrel monkeys is more dependent upon locomotor behavior than is the DR performance of normal squirrel monkeys.

The interaction of the cue situation with the effect of delay introduction was less effective in determining DR performance level when prefrontal monkeys were restrained during testing. Buddington et al. (1969) reported that when monkeys were unrestricted during testing, prefrontal performance was comparable to that of normals on the first DR test if both cubes were illuminated during the delay, but was deficient if both cubes were darkened. In the present investigation for monkeys restrained during testing, prefrontal performance also appears to be more comparable to that of normals on the first DR test when both cubes were illuminated rather than unlit during the delay (see Figure 2). This tendency was not verified by the statistics however. The lack of a significant four-way interaction, in conjunction with the significant L X T interaction, necessitates the conclusion that prefrontal performance did not vary as a function of either the cue situation or sequence of DR tests in the present study.

Intratrial Cue Observation

General considerations.--A test-trial was comprised of distinct but contiguous time periods. Each trial began with a two-second observation time during which both of the stimulus cubes were unlit. Immediately following this was a two-second cue period when one of the cubes was illuminated while the other remained darkened. At the end of the cue period, for the DT and STM tests, a transparent door separating the monkey from the stimulus cubes was removed and the monkey could respond. For DR testing, however, the cue period was immediately followed by a two-second delay period with both cubes either illuminated or unlit. A response was permitted at the end of the delay period during DR testing.

Observation period.--During the observation period that began each trial, all animals viewed the stimulus cubes. Typically, discriminanda observations were rapidly alternated from one cube to the other during this period. There were, however, frequent observations of the test environment which were not directed towards either stimulus cube. On the average therefore, only 40 to 60 percent of the two-second observation period was spent actually viewing the stimulus cubes. The alternate observation of the two stimulus cubes continued into the cue period until the illuminated (rewarded) stimulus cube was first observed. Behavior during the observation period was therefore conceived of as being directed towards a search for the rewarded cube. The efficiency of prefrontal and normal search behavior was

assessed in terms of the latency for the first rewarded cube observation during the cue period (see Figure 3). Cube observations in this, and all subsequent analyses, were defined on the basis of frame by frame inspection of the motion picture records from testing. When a monkey viewed the stimulus cube he typically appeared as is indicated, semi-schematically, in Figure 1. The absence of significant effects from either of the statistical analyses for this latency measure indicates that search behavior did not vary as a function of lesion or testing conditions. It is therefore concluded that this aspect of intratrial behavior is not related to either the DR, or the overall performance deficit of prefrontal monkeys.

Cue period.--After the initial rewarded cube inspection, the monkeys typically made subsequent alternating observations of the negative (unrewarded) and positive (rewarded) cubes throughout the remainder of the cue period. Cue observations were quantified for each trial in terms of the number of motion picture frames in which the monkey observed the rewarded and unrewarded cue.

The significant cue-contingency main effect for the analysis of discriminanda observation during the cue period on DT indicates that the rewarded cube was observed more than the negative stimulus on both the first and last twenty trials of this test. The significant C X TR interaction, however, shows that the preference for positive cube observation increased greatly from the first to the last twenty

trial block. The lack of a significant TR main effect, however, indicates that the total amount of cue observation was the same for the first and last twenty trials of DT. It is therefore concluded that as DT is mastered the amount of rewarded cube inspection increases while there is a concomitant decrease in the amount of negative cube observation. Considering that all animals were trained with two darkened cubes during the shaping procedure, it is suggested that the slight preference for positive cube observation during the first twenty DT trials resulted from the novelty of the illuminated cube in its debut as an environmental stimulus. Finally, prefrontal operates were not statistically differentiable from normal controls in their intratrial cue observations on DT. This result agrees with the trials-to-criterion data where prefrontal performance was also statistically undifferentiable from that of normal controls.

The average total amount of discriminanda observation during STM (12.7 frames per trial) was less than during the last twenty trials of DT (13.3 frames per trial). As indicated by the significant task main effect for the analysis of discriminanda observation during the cue period of STM and DR, the average total amount of cube observation for DR (11.1 frames per trial) was less than that for STM. Finally, the significant trials main effect indicates that the amount of cue observation also decreased from the first to the last twenty trials for all tests. It is suggested that the decreased amount of stimulus observation, from DT to STM

to DR, reflects habituation to the general conditions of the test procedure. It is not unlikely, considering the basic similarity of the individual test procedures, that a learning-set for cue observations was developed as the animals progressed through the testing sequence. That the amount of discriminanda observation also decreased from the first to the last twenty trials is interpreted as indicating that "habituation" to the conditions of each test also occurred during acquisition. The significant task by trials interaction indicates that decrease in amount of cue observation from the first to the last twenty trials was greater for the DR tasks than for the STM tests. Considering that a much greater period of time (in terms of the number of trials to criterion) was spent on DR testing than on STM, it is concluded that habituation to the test conditions was greater during DR than during STM testing.

Approximately 70 percent of the total cue observation during the last twenty DT trials was directed towards the rewarded cube. The significant reward main effect for the analysis of observations during the cue period of STM and DR indicates that there was an overall preference for positive cue orientations on these tasks. More precisely, an average of 71 percent of the total observations were directed towards the positive cue during STM and DR testing. The significant task reward interaction shows that the percentage of positive cue orientations was greater for STM (73 percent) than DR (70 percent). Furthermore, the

significant task-trials reward interaction indicates that the percentage of rewarded cube observations increased from the first (70 percent) to the last (75 percent) twenty trials on STM, but decreased slightly from the first (70 percent) to the last (69 percent) twenty DR test-trials. These results support the conclusion that the preference for positive cue observation that was established during DT was maintained with little variation throughout STM and DR testing.

As indicated by the significant stimulus main effect, there was a greater total amount of observation on STM and DR when both cubes were darkened at the end of the cue period. The significant order stimulus cue-contingency interaction shows that there was a greater difference between positive versus negative cue orientations when both cubes were darkened for Group A monkeys. Group B monkeys, however, showed the greatest difference between positive and negative cube orientations when both cubes were illuminated at the end of the cue period. Finally, the significant lesion stimulus trials interaction revealed that there was a slight decrease from the first to last twenty trials in the total amount of cue orientations for prefrontal monkeys when they were tested on STM and DR with the both cubes darkened stimulus situation. For normal monkeys, however, there was a slight increase in total observation from the first to the last twenty test trials for the both cubes darkened STM and DR tasks. These results were not paralleled in the trials-to-criterion data. In particular, there was no significant stimulus main effect

and the performance of the monkeys was therefore similar for both of the cue situations during STM and DR testing. Also, there was no significant main effect or interaction involving the order factor, and the trials-to-criterion performance did not differ between Groups A and B during the STM and DR tasks. Finally, there was no significant difference between prefrontal and normal monkeys in the overall trials to criterion performance for the both cubes darkened stimulus situation. It is concluded therefore that the variations of intratrial observation indicated by the significant S, O X S X C, and L X S X TR effects reflect minor adaptations to the changes in overall performance level that were described for the trials-to-criterion data.

Delay period.--The significant cue-contingency main effect for the analysis of cue observations during the delay period, indicates that the rewarded cube was observed more than the negative cube throughout DR testing. More specifically, an overall average of 69.5 percent of the total cue observation during the delay period was directed toward the rewarded stimulus, and it should be noted that this figure is virtually identical to the percentage of positive cube observation during the cue period. While the significant trials main effect shows that the total amount of cue observation decreased from the first to the last twenty trials, the absence of a significant TR X C interaction indicates that the preference for positive cue observation was present during the first twenty DR test trials. It must be concluded,

therefore, that a preference for positive cube orientation during the delay does not develop as a result of DR training but is fully present at the first introduction of the delay into the testing procedure.

An inspection of the cell means for the significant five-way interaction revealed an overall pattern for cue observation during the delay period. There was an overall decrease in the total amount of discriminanda observation, from the first to last twenty test-trials, as was previously indicated in considering the T main effect. The relative proportion of rewarded and unrewarded cue observation, however, tended to be constant on the first and last twenty trials. The most notable exception to this general trend was for the Group A prefrontal operates on their first DR test with the darkened cube stimulus configuration. During the first twenty trials the proportion of positive cube observations for this group of prefrontals was decreased to 62 percent from the overall average of 70 percent. By the last twenty trials however the proportion of observations for the rewarded stimulus was increased to 75 percent. This result is in accord with the deficient trials-to-criterion performance of this prefrontal group on their first DR test (see Figure 2, Group A prefrontals for the both cubes darkened stimulus situation).

It is suggested on the basis of these results that, when their first DR test is with the cubes "off" situation, prefrontal squirrel monkeys have difficulty in maintaining

an orientation toward the rewarded cube during the delay period. This effect does not explain the overall DR impairment of prefrontal monkeys in that it is transitory and only appears for the first twenty test-trials. Furthermore, the pattern of cue observation for prefrontals under all other test conditions was similar to the overall pattern and did not match the variations in trials-to-criterion performance for the operated or normal groups. It is concluded therefore that the amount of rewarded and unrewarded cue observation is not related to the level of performance during DR testing.

Summary

It was not expected that the DR performance for monkeys restrained during testing would be different from the performance of prefrontal operates free to move about. Because the increased impairment of restricted prefrontal operates resulted in deficient performance throughout DR training, one of the original goals of this study was frustrated. It was originally intended that intratrial cue observations would be compared for operated and normal monkeys when prefrontal performance during initial DR testing was impaired for one of the cue situations but not the other. Cue situation interacted in this way with the effect of delay introduction for monkeys that were unrestrained during testing (Buddington et al., 1969). On the basis of this interaction those authors hypothesized that, in comparison to normal controls, prefrontal squirrel monkeys were more dependent

upon external cues for the guidance of their behavior when modification of response patterns was required during initial DR testing. Cue situation did not interact with the effect of delay introduction in the present investigation for restrained prefrontal monkeys and further study of this hypothesis was therefore abandoned.

If response modification occurred during initial DR testing, it was not reflected in the pattern of discriminanda observations during either the cue or delay periods. A preference for positive cube observations was established during DT and was subsequently maintained at a constant level throughout testing by both prefrontal and normal monkeys. There was, in fact, no consistant correlation between trials-to-criterion behavior and cube observation during either the cue or delay period for the DR tests, and it was therefore concluded that this measure was not related to DR test performance. The efficiency of search behavior during the observation period was also constant throughout DR testing for both normal and prefrontal monkeys.

Considering the drastic impairment of prefrontal performance during DR testing, it was surprising that no evident differences were found when the intratrial behavior of prefrontal and normal monkeys was compared. If prefrontal DR impairment derived from an increased perseverative tendency (e.g. Mishkin, 1964) or increased distractibility (e.g. Malmo, 1942), etc., it would be expected that one or another

aspect of the within-trial behavior for frontal monkeys would be greatly different from normal. This investigation shows, however, that prefrontal lesions have a much more subtle effect upon intratrial behavior than would have been expected on the basis of current hypotheses concerning the nature of prefrontal DR impairment.

The DR performance of prefrontal squirrel monkeys was shown to be more dependent upon locomotor behavior than was the performance of normal squirrel monkeys. This suggests that locomotor behavior is employed by the prefrontal monkey during DR testing to substitute for the lost function of his prefrontal cortices. Further experimentation is needed, however, to elucidate the functional role of locomotor behavior in the DR performance of prefrontal squirrel monkeys.

APPENDIX

Table 3. Cue Period: Individual Averages for the Number of Motion Picture Frames Showing Cube Observation

GROUP A

Task	Discrimination				Stimulus Manipulation			
Stimulus Cubes	One Cube Illuminated				Both Cubes Illuminated			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed*	R	N	R	N	R	N	R	N
Normals								
SM 366	7.0	7.8	12.5	2.8	12.4	5.0	13.0	1.6
SM 402	6.9	7.6	10.7	4.2	9.7	4.9	7.8	6.3
SM 413	8.0	3.6	9.0	5.1	8.3	5.5	7.4	4.4
Frontals								
SM 379	5.3	7.0	10.0	4.6	8.2	5.0	11.7	2.2
SM 412	5.5	5.4	10.0	3.9	9.1	3.4	8.9	3.0
SM 414	4.5	4.4	8.7	3.4	8.1	3.0	11.1	2.5

GROUP B

Task	Discrimination				Stimulus Manipulation			
Stimulus Cubes	One Cube Illuminated				Both Cubes Unlit			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed	R	N	R	N	R	N	R	N
Normals								
SM 384	3.5	3.7	7.1	6.1	6.8	5.4	8.8	4.2
SM 399	5.9	3.7	8.0	3.6	8.2	2.3	6.8	1.7
SM 445	6.3	6.5	9.7	3.3	10.6	2.2	9.3	8.9
Frontals								
SM 374	6.7	7.6	9.0	3.0	7.3	7.0	9.0	3.1
SM 410	5.4	7.1	10.9	3.4	8.8	3.5	10.0	3.5
SM 376	7.2	8.7	6.5	3.7	9.2	3.4	10.3	3.1

*Cue Observed: R=Rewarded Cube; N=Unrewarded Cube

Table 3. continued

GROUP A

Stimulus Manipulation				Delayed Response				Delayed Response			
Both Cubes Unlit				Both Cubes Unlit				Both Cubes Illuminated			
First 20		Last 20		First 20		Last 20		First 20		Last 20	
R	N	R	N	R	N	R	N	R	N	R	N
10.8	5.1	10.7	4.0	9.1	3.8	10.3	5.6	9.8	3.3	6.4	4.2
8.1	3.6	8.9	4.5	11.3	2.7	7.4	4.1	5.7	5.4	7.1	2.4
7.4	4.9	9.7	3.6	8.9	2.8	7.4	3.9	6.1	3.5	6.6	2.2
9.9	4.3	10.6	2.6	8.1	4.1	10.7	3.6	10.9	2.8	6.1	5.2
10.4	3.4	11.3	3.6	7.7	4.2	5.9	1.6	6.1	3.3	5.6	3.2
12.2	1.6	10.4	3.3	11.8	2.7	9.9	1.3	8.0	2.7	8.6	2.5

GROUP B

Stimulus Manipulation				Delayed Response				Delayed Response			
Both Cubes Unlit				Both Cubes Unlit				Both Cubes Illuminated			
First 20		Last 20		First 20		Last 20		First 20		Last 20	
R	N	R	N	R	N	R	N	R	N	R	N
7.9	3.2	9.0	2.5	7.7	3.5	6.4	3.5	7.6	3.6	9.5	3.1
5.7	1.6	7.7	2.6	8.0	2.0	5.6	1.8	5.4	1.9	6.5	2.3
9.4	2.7	8.9	1.8	8.9	4.3	8.9	2.0	7.3	3.3	6.4	2.2
10.7	4.3	10.8	2.9	6.6	4.3	7.6	1.4	9.3	6.7	6.4	2.8
7.3	3.0	8.8	2.6	8.3	3.2	5.0	3.6	6.4	4.4	5.3	5.6
9.3	2.4	9.0	3.5	9.6	1.7	9.1	3.3	10.4	3.8	4.5	3.0

Table 4. Delay Period: Individual Averages for the Number of Motion Picture Frames Showing Cube Observation

GROUP A

Task	Delayed Response				Delayed Response			
Stimulus Cubes	Both Cubes Unlit				Both Cubes Illuminated			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed*	R	N	R	N	R	N	R	N
Normals								
SM 366	9.0	2.2	8.9	2.2	8.4	3.0	8.7	1.0
SM 402	9.8	2.4	6.2	2.3	4.8	3.9	3.5	1.5
SM 413	7.4	3.0	6.8	2.8	6.3	4.0	6.6	3.6
Frontals								
SM 379	7.0	2.4	8.3	1.1	7.6	4.3	6.2	5.7
SM 412	5.8	4.8	4.0	3.2	4.5	3.5	1.9	3.6
SM 414	7.0	4.8	8.5	2.0	8.5	2.6	7.9	1.1

GROUP B

Task	Delayed Response				Delayed Response			
Stimulus Cubes	Both Cubes Illuminated				Both Cubes Unlit			
Trials Sampled	First 20		Last 20		First 20		Last 20	
Cue Observed	R	N	R	N	R	N	R	N
Normals								
SM 384	7.6	4.5	6.8	3.1	6.9	3.1	8.6	1.7
SM 399	5.0	4.1	4.3	2.9	4.9	1.7	6.2	1.2
SM 445	7.8	5.1	6.8	3.2	5.9	2.4	4.6	2.2
Frontals								
SM 374	8.6	2.0	7.5	0.8	6.4	4.2	6.2	1.0
SM 410	6.8	3.8	6.0	2.5	7.8	2.0	6.7	3.0
SM 376	7.4	3.9	8.0	4.4	8.3	4.0	4.4	3.3

*Cue Observed: R=Rewarded Cube; N=Unrewarded Cube

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BIOGRAPHICAL SKETCH

Roger Winton Buddington was born on June 13, 1943, in Bridgeport, Connecticut. His parents moved to Stratford, Connecticut in 1947 where he attended public school until he was graduated from Bunnell High School in 1961. He attended Fairfield University in Fairfield, Connecticut from 1961 until 1965 when he received his Bachelor of Arts degree with a major in Experimental Psychology. In September, 1965, he entered the University of Florida Graduate School in the Department of Psychology. He worked as a research assistant in the Division of Neurosurgery from 1965 to 1967, when he received the degree of Master of Arts with a major in Experimental Psychology. From 1967, until the present time he has held a Predoctoral Fellowship in the Center for Neurobiological Sciences of the University of Florida and has pursued his work toward the degree of Doctor of Philosophy.

Roger Buddington is married to the former Sharon Marie Cunha, and has two sons.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frederick A. King, Chairman
Professor of Neuroscience

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Charles J. Vierck
Associate Professor of Neuroscience

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Co-Director of Center for
Neurobiological Sciences
Professor of Psychology

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Wilse B. Webb
Graduate Research Professor

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Henry S. Pennypacker
Professor of Psychology

This dissertation was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

February, 1971

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